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Research

Unique and shared effects of local and catchment predictors over distribution of hyporheic organisms: does the valley rule the stream?

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Understanding and predicting the geographic distribution of taxa in hierarchical stream landscapes is a cornerstone of river ecology. A central issue is to tease apart the unique and shared effects of local and catchment predictors over species distributions. Here, we tested Hynes's influential hypothesis (1975, Baldi Memorial Lecture) that 'In every respect, the valley rules the stream'. We predicted that if catchment features exert a major control on in-stream local conditions, the shared effect of local and catchment predictors should largely surpass their unique effects. To test this prediction, we used logistic regression models and variation partitioning to quantify the unique and shared effects of local and catchment predictors on the distribution of two hyporheic crustacean taxa (Bogidiellidae, Amphipoda and Anthuridae, Isopoda) in streams of New Caledonia. We sampled the two taxa at 228 sites. At each site, we quantified nine local predictors related to habitat area and stability, sediment metabolism and water origin, and eight catchment predictors related to geology, area, primary productivity, land use and specific discharge. When analyzed separately, the two predictor types explained the same amount of model variation in occurrence in both taxa. When analyzed jointly, the shared effects of the two predictor types explained twice as much model variation as the unique effect of each. The overriding contribution of shared effects was notably due to controls exerted by catchment area and geology on local habitat size and sediment metabolism, respectively. For both taxa, a model with only these two catchment predictors provided occurrence distribution as reliable as models containing only local predictors or both predictor types. Our findings pave the way for predicting reliably from catchment predictors alone the geographic distribution in local occurrence of taxa in difficult-to-access habitats and landscapes, such as here the hyporheic zone of tropical streams.

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Keywords: hierarchical partitioning, hyporheic zone, New Caledonia, river landscape, spatial scale, species distribution model, subterranean crustaceans

Introduction

Predicting species geographic distributions has become a key priority in the face of the ongoing biodiversity crisis (Lenoir et al. 2020, Liu et al. 2020). A major goal consisted of identifying how environmental factors at multiple spatial scales act upon processes shaping species occurrence (Elith and Leathwick 2009, Fournier et al. 2017). In species distribution models (SDM), this goal is commonly achieved by assembling a set of scale-specific predictors that may affect the distribution of species at the landscape and local habitat scales (Domisch et al. 2015, Araújo et al. 2019). The outcome in terms of explicative and predictive powers depends on the interdependency among local and landscape factors. On the one hand, a strong co-variation among local and landscape factors can make teasing apart their relative influence difficult. On the other hand, a strong co-variation may be beneficial to make accurate local predictions from landscape factors alone. The picture above is further tangled because the way broad and fine-scale factors interact is often landscape-dependent, with many landscape factors including topographic position and land cover having cascading effects on local conditions (With 2019, Chauvier et al. 2021). These across-scale effects are expected to be particularly important in determining species distributions in stream landscapes, given that most material (sediment, organic matter and nutrients) that contributes to the heterogeneity and trophic resources of in-stream local habitats derives from adjacent terrestrial catchments (Allan and Johnson 1997, Harvey and Altermatt 2019).

The idea that in-stream habitat conditions are strongly influenced by catchment factors was central to Hynes's eloquent plea (1975, Baldi Memorial Lecture) that 'In every respect, the valley rules the stream'. Hynes' intuition has been supported by decades of research, quickly becoming a central tenet of freshwater ecology (Fausch et al. 2002, Allan 2004, Frimpong et al. 2005, Peterson et al. 2011). Catchment factors such as climate, geology, topography and soil cover largely control the supplies of water, sediment and nutrients, which determine local in-stream physical and chemical conditions (Frissell et al. 1986, Snelder and Biggs 2002). Meantime, SDMs have increasingly incorporated a hierarchical landscape framework of streams in which species distributions are shaped by factors operating across multiple scales from the entire catchment upstream of a site to the local site (Stewart-Koster et al. 2013, Kuemmerlen et al. 2014, Wellemeyer et al. 2019). However, most modelling studies incorporating multi-scale predictors have focused on determining whether a species distribution was best explained by local-scale versus catchment-scale predictors (Chee and Elith 2012, Domisch et al. 2015), even though the latter are often included to represent indirect or missing local-scale predictors (Johnston et al. 2017, Caradima 2020).

A better integration of the stream hierarchical framework into SDMs would benefit from considering both the unique and shared effects of catchment and local factors. If, as hypothesized by Hynes (1975), catchment-scale factors exert a disproportionate influence on many of the in-stream local factors affecting a species distribution, then, the shared effects of the two predictor types should exceed their unique effects. An expected outcome of the dominance of shared effects is that distal catchment factors could equally well predict species occurrences as proximate local factors. In theory, catchment factors alone may even provide a better prediction than local factors if they have unique effects on species distributions and their shared effects explain all the effects of local factors (i.e. local factors have no unique effects). Making local predictions from catchment predictors alone would be especially relevant for filling knowledge gaps in the distribution of species confined to riverine habitats for which monitoring-based local environmental data are lacking.

Hyporheic habitats – the water-saturated sediments beneath and alongside the stream bed through which stream water flows – are major structural, functional and biological components of river ecosystems (Malard et al. 2002, Ward 2016). They contain diversified assemblages of invertebrate species including hyporheic specialists that complete their entire life cycle exclusively within the streambed sediments (Gibert et al. 1994). Catchment effects on the structure and function of hyporheic habitats are potentially more pronounced than for surface stream habitats. Bedrock lithology of the catchment and erosion influence the amount, pore size, permeability and continuity of streambed sediments, and hence, the area, suitability and connectivity of hyporheic habitat patches (Malard et al. 2017, Shrivastava et al. 2020). Burial of allochthonous organic matter into the streambed affects sediment metabolism because it stimulates microbial respiration, causing oxygen depletion and setting up strong redox gradients along hyporheic flow paths (Pereda et al. 2017, Reeder et al. 2018). Direct hydrological exchanges between streambed sediments, soils and lateral aquifers exert major control on flow permanency, thermal regime and cycling of organic matter within hyporheic habitats (Malcolm et al. 2005, Wondzell and Gooseff 2013). Despite extensive documentation of hyporhei zone–catchment interactions, there have been no attempts to model the distributions of hyporheic taxa using a combination of catchment and local predictors.

We used logistic regression models and variation partitioning to quantify the unique and shared effects of catchment and local predictors on the distribution of two hyporheic crustacean taxa (Bogidiellidae, Amphipoda and Anthuridae, Isopoda) in streams of New Caledonia. The New Caledonian Archipelago is one of the world's biodiversity hotspots (Myers et al. 2000). Beside its heterogeneous topography, the main island (Grande Terre) stands out among islands because of the areal importance of peridotite rocks, which cover about one third of the island (Pillon et al. 2021). There is ample evidence that nutrient-poor and metal-rich ultramafic soils developing on peridotite have contributed disproportionately to the distinctiveness and distribution of terrestrial plants and animals (Nattier et al. 2013, Isnard et al. 2016). Although stream organisms have been comparatively less studied, their distributions have also been suggested to reflect the influence of peridotite rocks on stream features (Mary and Marmonier 2000, Mary 2002, Espeland and Johanson 2010). Hence, we predicted that if catchment-scale factors, more specifically the areal extent of peridotite, exerted a major control on in-stream local conditions, the shared effects of catchment and local predictors on the distribution of hyporheic taxa should largely surpass their unique effects. Due to the expected dominance of shared effects, we further predicted that SDMs based only on catchment predictors would provide occurrence distributions as accurate as models containing local predictors alone or both predictor types.

Material and methods

Presence/absence data

We collected presence/absence data for Bogidiellidae and Anthuridae from 228 freshwater hyporheic sites during a scientific expedition to New Caledonia (Fig. 1). Bogidiellidae Hertzog, 1936 is a species-rich family of subterranean amphipods (Koenemann and Holsinger 1999). New Caledonian bogidiellids had previously been reported from a single littoral cave in Lifou Island (Jaume et al. 2007) and two hyporheic sites on the main island (Mary and Marmonier 2000). The anthurids collected during the expedition belonged to the subterranean genus *Stygocyathura* Botosaneanu & Stock, 1982. This genus had previously been reported from only two coastal, interstitial sites in New Caledonia (Wägele 1982). All bogidiellid and anthurid specimens collected during the expedition were blind and depigmented. Although these specimens undoubtedly belong to several new species, following Qiao et al. (2017) we assumed that these species shared similar ecological traits and modelled their distribution at the family (Bogidiellidae) and genus level (*Stygocyathura*, thereafter referred to as anthurids).

We carried out sampling in November 2016, November 2017 and July 2018, during low flow periods. We obtained hyporheic samples by hammering a perforated pipe to a depth of 60 cm below the streambed (Boulton et al. 2003). We used a hand piston pump to extract 10 l of hyporheic water and sediments that we elutriated and filtered through a 150-µm-mesh net. We immediately searched for the presence of bogidiellids and anthurids in the filtered sample using a field-dissecting microscope. When one or both taxa were not present in the first replicate sample, we collected up to four replicate samples to ascertain their absence at a site. All filtered samples were preserved in 96% ethanol and were again processed under a laboratory dissecting microscope to check for the presence/absence of bogidiellids and anthurids.

Local predictors

We used nine local predictors to describe in-stream habitat conditions: river width, specific conductance, dissolved oxygen (DO), redox potential, pH, temperature of hyporheic water, mean annual air temperature, elevation and stream slope. We used one-time measurements of physio-chemical parameters assuming that temporal variations in stream water chemistry and temperature were low at a depth of 60 cm into

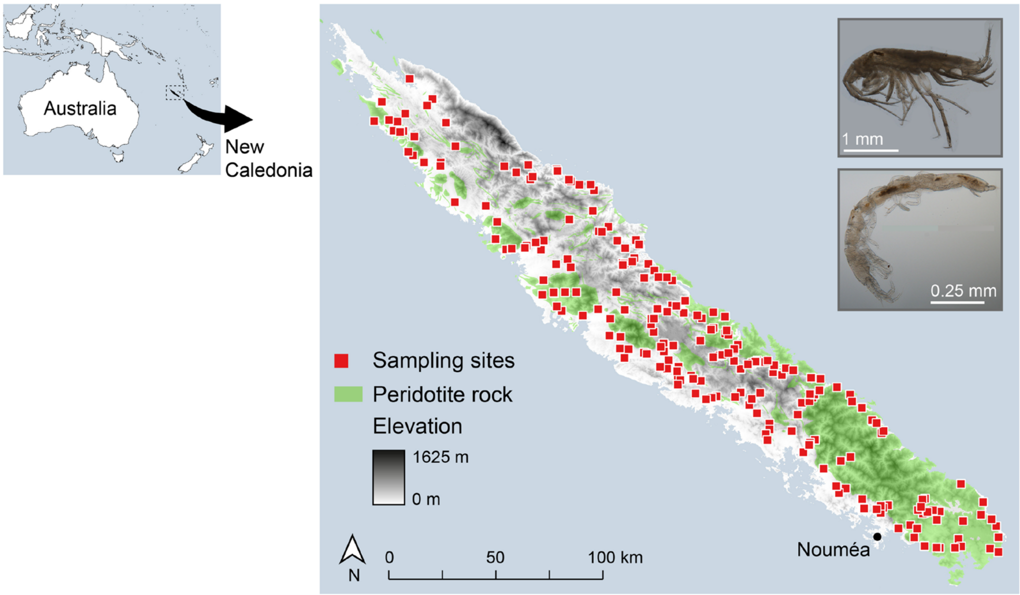

Figure 1. Distribution of sampled hyporheic sites (n = 228) in streams of New Caledonia. The right upper and lower photos show blind and depigmented Bogidiellidae (Amphipoda) and Anthuridae (Isopoda), respectively.

the streambed sediment of tropical streams. We measured river width as the width of the area occupied by low-flow channels and unvegetated gravel bars (Bertrand and Liébault 2019), and used it as a surrogate of the sedimentary habitat area available for hyporheic organisms. We measured specific conductance, temperature, pH, redox potential and DO of hyporheic water with a multi-parameter probe (Odéon, Aqualabo, France). Specific conductance is a proxy for the origin of water; it increases with increasing residence time of water in the subsurface, either in the hyporheic zone or in lateral aquifers hydrologically connected to it (Cox et al. 2007). DO, redox potential and pH are indicators of hyporheic sediment metabolism: they are expected to be lower in hyporheic sediments that receive higher organic matter supply because microbial respiration would rapidly consume terminal electron acceptors along hyporheic flow paths (Malard et al. 2002, Reeder et al. 2018). In addition to one-time measurement of hyporheic water temperature, we extracted mean annual air temperature from the WorldClim 2 dataset (30 arc-second resolution, Fick and Hijmans 2017) as a surrogate of mean annual stream water temperature. We obtained elevation of the sites from a 10-m resolution digital elevation model (DEM) of New Caledonia. We computed river slope for every 50 m-long stream segment of the digital stream network of New Caledonia.

Catchment predictors

We used eight predictors to describe catchments: catchment area, areal proportion of peridotite, three land cover predictors, normalized difference vegetation index (NDVI), mean annual precipitation and low flow specific discharge. We produced a digital stream network of New Caledonia using a 10-m-resolution DEM. The network contained 29 405 nodes regularly located at every 0.1-km^2 increase in catchment area from a minimum catchment area of 5 km^2. We computed each predictor for the entire upstream contributing catchment area associated with each sampled site. We computed the areal proportion of peridotite rocks from the 1:50 000 geological map of New Caledonia. We derived the three land cover predictors from the 1:12 000 land cover map of New Caledonia using a procedure described in the Supporting information. Values of land cover predictors 1 and 2 increased with increasing proportion of bare soil and decreased with increasing proportion of mature forests and herbaceous vegetation, respectively. Values of land cover predictor 3 increased with increasing proportion of shrubs. We used mean NDVI to assess differences in above-ground biomass among catchments. We computed the index from 12 NDVI raster files available at a resolution of 250 m over the period 2000–2011. From WorldClim 2, we extracted mean annual precipitation averaged over the upstream contributing catchment area associated with each site. We obtained the low flow specific discharge for each catchment, defined as the average daily flow exceeded 355 days per year, from hydrological models by Romieux and Wotling (2016). We performed all geospatial analyses in *ArcGIS* 10.2.2 (Esri, Redlands, California, USA).

Statistical analysis

Unique and shared effects of local and catchment predictors

We compared the abilities of local and catchment predictors to explain and predict the occurrence of bogidiellids and anthurids using logistic regression models. Prior to modelling, we measured multicollinearity within and between the two types of predictors with Pearson's r correlation coefficients and variance inflation factors (VIFs). Then, we used a two-step procedure to quantify the unique and shared effects of catchment and local predictors. In step 1, we assessed separately the amount of variation explained by the two predictor types and used multi-model inferences to quantify the importance of each predictor within its type (Burnham and Anderson 2002). We compared models using Akaike information criterion corrected for small sample size (AICc). For each predictor type, we ran all possible models and only kept those models with a ΔAICc (AICc of the model − lowest AICc model) of less than 5. To assess the importance of each predictor within its type, we used the sum of the AICc weights of the models in which the predictor was retained and the proportion of explained variation associated with the predictor (i.e. the amount of deviance reduction). We selected only those predictors with an AICc weight higher than 0.7 to build the local and catchment models. For illustration purposes, we displayed the relationships between the probabilities of occurrence and each selected predictor by computing those probabilities over the predictor's observed range from a simple logistic regression containing only that predictor as an explanatory variable.

In step 2, we evaluated the amount of variation explained by the two types of predictors for both taxa in a joint model containing the best set of predictors selected separately for each type of predictor in step 1 (i.e. the predictors of the local and catchment models). As in step 1, we used multi-model inference to evaluate the relative importance of predictors. Next, we used variation partitioning in the context of logistic regressions (Chevan and Sutherland 1991, Mac Nally and Walsh 2004, Walsh et al. 2004, de Araújo et al. 2014) to assess the unique and shared effects of the two predictor types. Variation partitioning in the context of logistic regressions is performed using pseudo R^2. These are surrogates of explained variance in normal error models, in that they all represent the proportion of variation explained by the predictors. In this study, we performed variation partitioning using the likelihood ratio pseudo R^2 (Cohen et al. 2002), the Nagelkerke's pseudo R^2 (Nagelkerke 1991), MacFadden's pseudo R^2 (McFadden 1974, de Araújo et al. 2014) and Tjur's pseudo R^2 (Tjur 2009). Unique effects correspond to the variation that is attributable purely to a given predictor type. In the framework of hierarchical stream landscapes, the unique effects of local and catchment predictors represent the direct influence of these two predictor types on the local occurrence of species (Fig. 2). Shared effects correspond to the variation attributable to the two predictor types. They include the indirect influence of catchment predictors on the local occurrence of species: catchment predictors influence

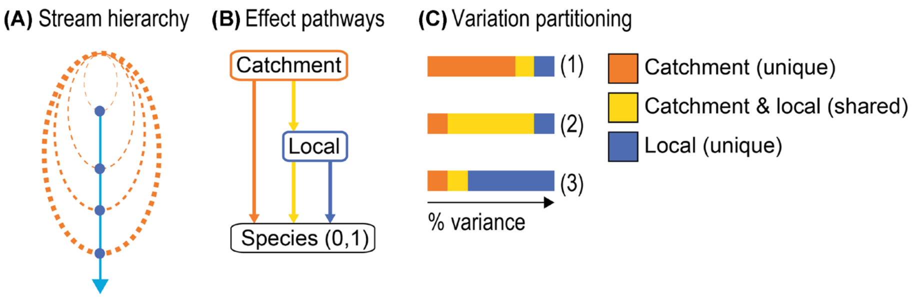

Figure 2. Conceptual framework for partitioning unique and shared effects of catchment and local predictors on species distribution in hierarchical stream landscapes. (A) Spatially overlapping catchments (orange broken lines), each draining to a single site (dark blue dots), accumulate hierarchically in a downstream direction (the light blue arrow represents the stream). (B) Direct and indirect pathways how catchment and local predictors influence local occurrence of a species (0: absence; 1: presence). (C) Expected relative proportions of variation attributed to the unique effects of catchment predictors (orange bars), unique effects of local predictors (blue bars) and shared effects of catchment and local predictors (yellow bars). Local occurrences of a species are predominantly driven by (1) direct effects of catchment predictors, (2) indirect effects of catchment predictors on in-stream local conditions or (3) direct effects of local predictors. Hynes's hypothesis (1975) that 'in-stream local habitat predictors potentially affecting a species' distribution are strongly influenced by catchment predictors' should result in variation partitioning as shown in (2).

in-stream local factors, which in turn affect a species distribution (Fig. 2).

Model evaluation and predictions

We tested for the presence of spatial autocorrelation in the residuals of the three models (local, catchment, joint) by examining the distance decay of the Moran's I statistic (Moran 1948). Spatial autocorrelation may be due to the omission of a spatially autocorrelated predictor or to dispersal (Dormann et al. 2007). We created a neighborhood matrix using the variance stabilizing S-coding scheme (Tiefelsdorf et al. 1999) and computed the correlograms for 20 great-circle distance classes, each containing 5% of pairwise comparisons between sites. We used a randomization test with 1000 iterations to assess the significance of Moran's I in each distance class under the null hypothesis of a spatially random distribution.

Using the full data set for training, we evaluated differences in the predictions among the three models by generating the confusion matrix (true positives and negatives, false positives and false negatives). We quantified the number of sites for which the three models and any combination of two models provided the same predictions.

We used a repeated random subsampling procedure to evaluate the predictive performances of all models (Franklin 2010). Given that we had presence/absence data, we assessed performance with the area under the curve (AUC). Models are generally considered as acceptable when AUC is above 0.7 (Hosmer and Lemeshow 2000). For 1000 iterations, we randomly sampled 75% of the data for training the models and we used the remaining 25% for evaluating the predictive performances, yielding 1000 AUC values for the local, catchment and joint models. We used pairwise t-tests with Bonferonni–Holm correction to test for differences in AUC between models. Finally, we used the catchment models to make predictions to unsurveyed locations in New Caledonia. We attributed each of the 29 405 nodes of the digital stream network with the predictors of the catchment models so that predictions could be made locally at the spatial extent of the main island.

We performed multi-model inference using the 'MuMIn' package (Barton 2019) in R ver. 3.6.3 (<www.r-project.org>). We calculated pseudo R^2 and VIFs using the 'DescTools' package (Signorell et al. 2021) and the AED script from Zuur et al. (2009), respectively. We calculated AUCs with the 'dismo' package (Hijmans et al. 2017) and performed spatial autocorrelation analyses with 'fields' (Nychka et al. 2017) and 'spdep' packages (Bivand et al. 2013).

Results

Relationships among predictors

We found significant relationships among predictors both within and between the two types of predictors (Supporting information). Within catchment predictors, the proportion of bare soil and NDVI increased ($r = 0.48$) and decreased ($r = -0.60$), respectively, with the areal proportion of peridotite. Low flow specific discharge was positively correlated with the areal proportion of peridotite ($r = 0.56$). Within local predictors, DO was positively correlated with redox potential ($r = 0.66$) and pH ($r = 0.63$), whereas specific conductance was positively correlated with mean annual air temperature ($r = 0.42$) and negatively with elevation ($r = -0.66$). Between local and catchment predictors, river width increased with increasing catchment area ($r = 0.56$). DO and pH increased with increasing proportion of peridotite in the catchment ($r = 0.63$ and $r = 0.62$, respectively) and decreased with increasing NDVI values ($r = -0.44$ and $r = -0.43$, respectively) (Fig. 3). DO was positively correlated ($r = 0.43$), and specific conductance ($r = -0.53$) and mean annual air temperature ($r = -0.50$) negatively correlated, with low flow specific discharge. VIFs were mostly below 5, the highest values

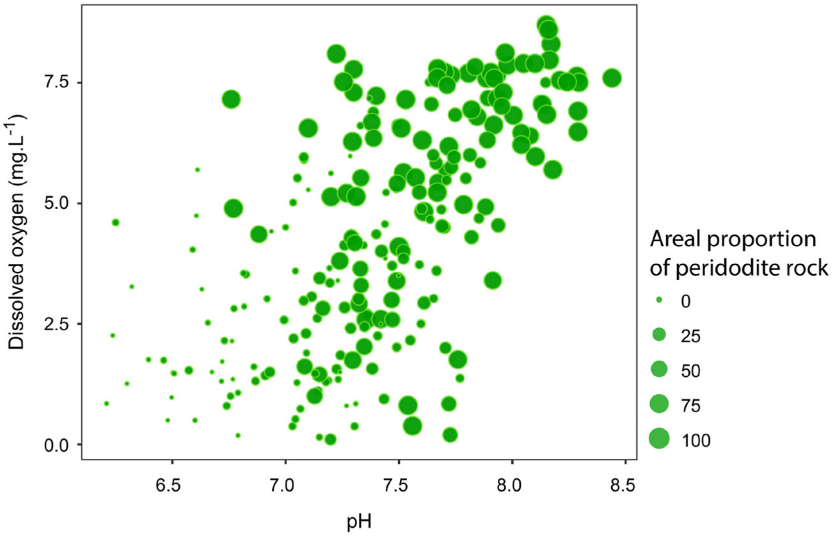

Figure 3. Relationship between dissolved oxygen and pH of hyporheic water and the areal proportion of peridotite rock in the upstream contributing catchment area associated with 228 hyporheic sites in streams of New Caledonia.

being those of NDVI (6.8), land cover 1 (5.6), DO (4.5) and proportion of peridotite (4.3) (Supporting information).

Unique and shared effects of local and catchment predictors

Local and catchment models

AICc values for the local, catchment and joints models were 272.07, 270.23 and 261.29, respectively, for the bogidiellids, and 260.94, 262.69 and 256.51, respectively, for the anthurids. The local and catchment models explained a similar proportion of model variation in occurrence of taxa, although the proportion was higher for bogidiellids (local: 17.9%; catchment: 16.5%) than for anthurids (local: 9.4%; catchment: 8.7%). Of the nine candidate predictors considered in the local models, only five had an AICc weight > 0.7; weights of the remaining predictors were < 0.3 (Table 1, Supporting information). Redox potential and river width explained the highest proportion of model variation for the bogidiellids (7.52 and 3.83%, respectively) and they were the only predictors retained in the model for anthurids. The probability of occurrence of both taxa increased with increasing values of these two predictors (Fig. 4, Supporting information). We retained the remaining predictors – pH, stream slope and specific conductance – in the local model for bogidiellids. However, these predictors cumulatively accounted for a much lower proportion of model variation (6.48%) than that explained together by river width and redox potential (11.35%).

Of the eight candidate predictors considered in the catchment models, the areal proportion of peridotite and catchment area were the only predictors retained to explain both the occurrence of bogidiellids and anthurids (AICc weight > 0.7, Table 1). All other catchment predictors had weights $\leq$ 0.4, except the third land cover predictor for the anthurids (AICc weight = 0.57, Supporting information). In both taxa, the areal proportion of peridotite disproportionately contributed to the model variation: it explained 11.2 and 4.4 times more variation than the second best predictor, catchment area, for the bogidiellids and anthurids, respectively. The probability of occurrence of both taxa increased with increasing areal proportion of peridotite and catchment area (Fig. 4, Supporting information).

Joint model and variation partitioning

Of the seven predictors retained in the local and catchment models for bogidiellids, four – areal proportion of peridotite, stream width, redox potential and specific conductance – had an AICc weight $\simeq$ 1 in the joint model (Table 1). For the anthurids, two of the four predictors selected in the local and catchment models – the areal proportion of peridotite and stream width – had an AICc weight $\simeq$ 1 in the joint model. All other predictors had weights < 0.5, slope, catchment area and pH for the bogidiellids, and redox potential and catchment area for the anthurids, and were excluded from the best joint models (i.e. the models with the best AICc). Among the predictors with an AICc $\simeq$ 1, the areal proportion of peridotite made by far the largest contribution to the explained variation (Table 1). It alone explained 2.2 times more variation than that explained together by stream width, redox potential and specific conductance in the bogidiellid model and 1.6 times more variation than river width in the anthurid model.

Variation partitioning using either the likelihood ratio pseudo R^2 or Nagelkerke's pseudo R^2 showed that the shared effects of local and catchment predictors largely exceeded their unique effects (Fig. 5A). The shared effects of the two predictor types explained 1.9 and 2.4 times more variation than the unique effects of local and catchment predictors, respectively, for the bogidiellids, and 1.5 and 1.9 times, respectively, for the anthurids. Variation partitioning with MacFadden's pseudo R^2 and Tjur's pseudo R^2 confirmed

Table 1. Summary results of logistic regressions for testing local and catchment predictors of the occurrence of bogidiellids and anthurids in the hyporheic zone of New-Caledonia streams. For local and catchment models, only those predictors with an Akaike information criterion corrected for small sample size (AICc) weight > 0.7 were retained (Supporting information). All predictors retained in the local and catchment models were considered in the joint models. Proportions of explained variation (i.e. proportion in reduction of deviance), coefficient parameters and p values are from the local and catchment models with the lowest AICc and from the joint model including all the predictors retained in the best local and catchment models. In bold, significant p values for the predictors.

Model	Taxa	Predictors	AICc weight	Explained variation (%)	Coefficient	p
Local	Bogidiellidae	Intercept			–9.31	$3.4e^{-04}$
		Redox potential	1.00	7.52	0.01	**$2.4e^{-04}$**
		Stream width	1.00	3.83	0.02	**$3.2e^{-03}$**
		pH	0.86	3.92	0.87	**$1.8e^{-02}$**
		Slope	0.83	1.30	12.78	**$9.1e^{-02}$**
		Sp conductance	0.79	1.26	0.002	**$5.3e^{-02}$**
	Anthuridae	Intercept			–2.45	$1.72e^{-06}$
		Stream width	1.00	6.89	0.02	**$1.33e^{-04}$**
		Redox potential	0.86	2.49	0.005	**$1.26e^{-02}$**
Catchment	Bogidiellidae	Intercept			–1.42	$5.21e^{-07}$
		Peridotite	1.00	15.09	0.03	**$6.26e^{-11}$**
		Catchment area	0.79	1.34	0.004	**$4.59e^{-02}$**
	Anthuridae	Intercept			–1,97	$4.38e^{-10}$
		Peridotite	1.00	7.15	0.02	**$4.10e^{-06}$**
		Catchment area	0.79	1.61	0.004	**$3.51e^{-02}$**
Joint	Bogidiellidae	Intercept			–2.81	$3.79e^{-01}$
		Peridotite	1.00	15.09	0.02	**$2.09e^{-04}$**
		Redox potential	1.00	2.24	0.01	**$4.09e^{-03}$**
		Sp conductance	1.00	1.56	0.003	**$1.15e^{-02}$**
		Stream width	0.97	3.07	0.02	**$3.84e^{-02}$**
		Slope	0.41	0.47	8.35	$2.65e^{-01}$
		Catchment area	0.32	0.14	0.002	$4.86e^{-01}$
		pH	0.25	0.02	–0.12	$8.00e^{-01}$
	Anthuridae	Intercept			–2.47	$4.91e^{-06}$
		Peridotite	1.00	7.15	0.01	**$1.04e^{-02}$**
		Stream width	1.00	4.55	0.02	**$8.79e^{-03}$**
		Redox potential	0.49	0.71	0.00	$1.70e^{-01}$
		Catchment area	0.27	0.02	0.00	$8.30e^{-01}$

these results, with shared effects consistently higher than unique effects (Supporting information).

Model evaluation and predictions

For both taxa and the three models, we found no evidence of spatial autocorrelation in the model residuals. Moran's I was not significant in any of the 20 distance classes of the correlograms (Supporting information).

The local, catchment and joint models provided the same predictions at 166 (73%) and 201 (88%) of the 228 sampled sites for bogidiellids and anthurids, respectively (Supporting information). These congruent predictions among the three models included 128 and 154 true positives or true negatives, 16 and 2 false positives and 22 and 45 false negatives for the bogidiellids and anthurids, respectively. In both taxa, false positives and false negatives were associated with sites draining catchments having low and high areal proportions of peridotite, respectively. The three models had similar predictive performances in both taxa. Mean AUC values (± standard deviation) for the local, catchment and joint models were 0.74 ± 0.057, 0.76 ± 0.057 and 0.77 ± 0.054 for the bogidiellids, and 0.68 ± 0.07, 0.69 ± 0.07 and 0.70 ± 0.07 for the anthurids (Fig. 5B). These AUC values were significantly different among models within taxa (Pairwise t-tests, $p < 0.001$ for bogidiellids, $p < 0.05$ for anthurids).

Probabilities of occurrence of the two taxa for each of the 29,405 nodes of the digital stream network are illustrated in Fig. 6 and the Supporting information. They were derived from the catchment model after computing the areal proportion of peridotite and catchment area for each node. Although both taxa had a higher predicted probability of occurrence in stream reaches draining peridotite rock, anthurids were predicted to be considerably rarer, especially in upstream narrow reaches draining small catchment areas.

Discussion

Incorporating issues of scale into SDMs – specifically, here, the relative importance of unique and shared effects of scale-specific predictors – is key to understanding and predicting the distribution of species in hierarchical landscapes (Fournier et al. 2017, With 2019). This study is the first to model the distribution of hyporheic taxa using a combination of catchment and local predictors; it also represents one of the first attempts to apply SDM to subterranean

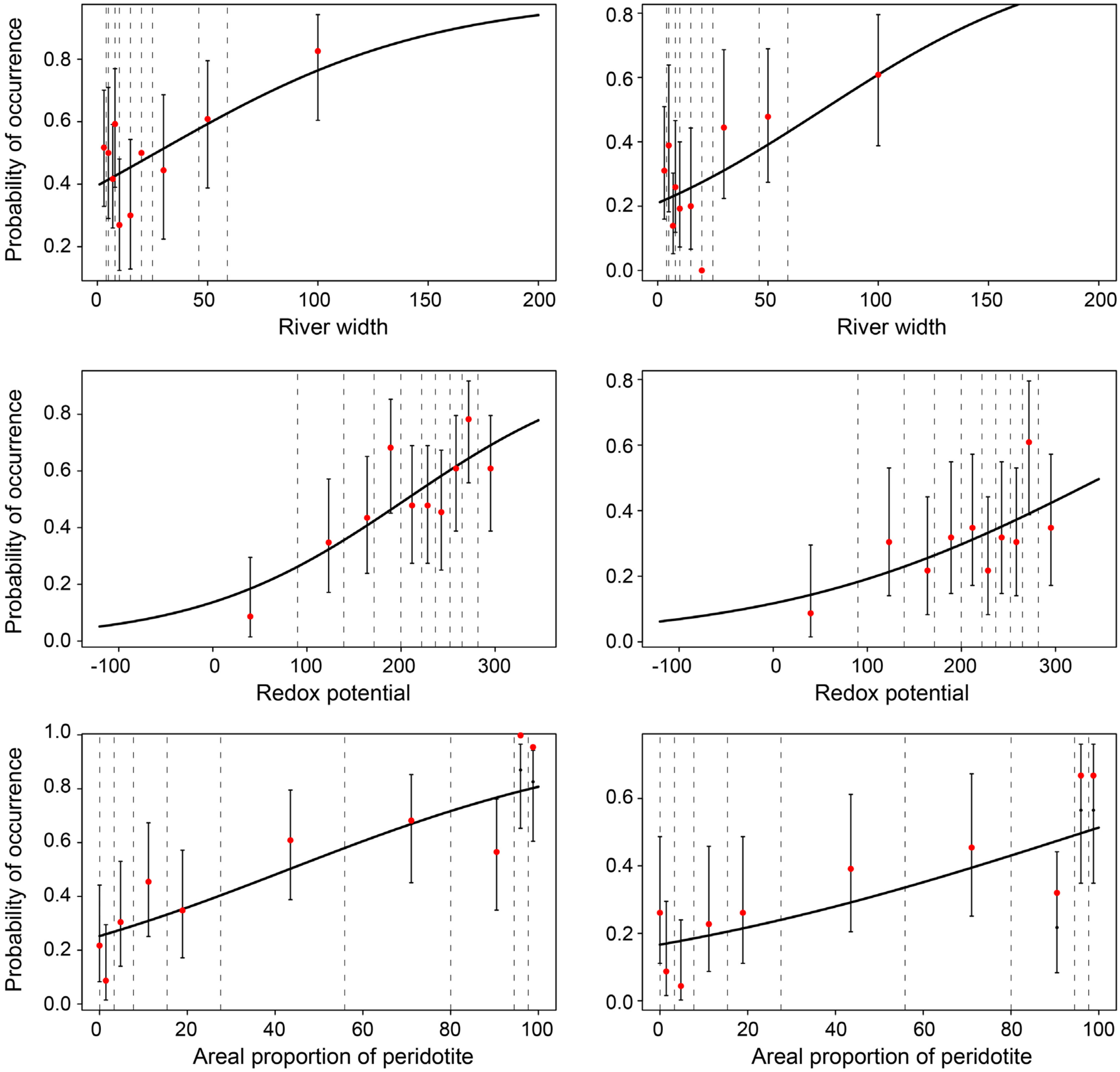

Figure 4. Relationships based on logistic regressions between the probability of occurrence of bogidiellids (lefts panels), anthurids (right panels) and river width, redox potential and the areal proportion of peridotite in the catchment. Broken lines delineate classes with equal numbers of sites used for calculating probabilities. Probabilities are plotted at the median of each class. Vertical bars show asymmetrical confidence intervals with continuity correction computed according to Newcombe (1998).

taxa outside temperate areas. Patterns of correlation among local and catchment predictors and the dominance of shared effects over unique effects were consistent with Hynes's hypothesis (1975). The overriding importance of indirect effects of catchment on species distributions (prediction 1) was essentially due to strong linkages between catchment area and local habitat size (i.e. stream width), and between catchment geology and sediment metabolism (i.e. redox potential, DO and pH). Due to the strong control of catchment attributes on in-stream habitat conditions, we further showed that a model based on catchment predictors alone provides occurrence predictions as reliable as models containing local predictors alone or both predictor types (prediction 2).

The dominance of shared effects on the distribution of stream organisms is an expected outcome of the co-variation among catchment and local predictors. Multicollinearity is likely to occur even though the most correlated predictors are excluded during model building (Dormann et al. 2013), a common practice in most studies. In the present study, no local predictors showed a Pearson's r correlation above 0.7 with catchment predictors and all VIFs, except two of them, were lower than 5, two thresholds commonly used to exclude

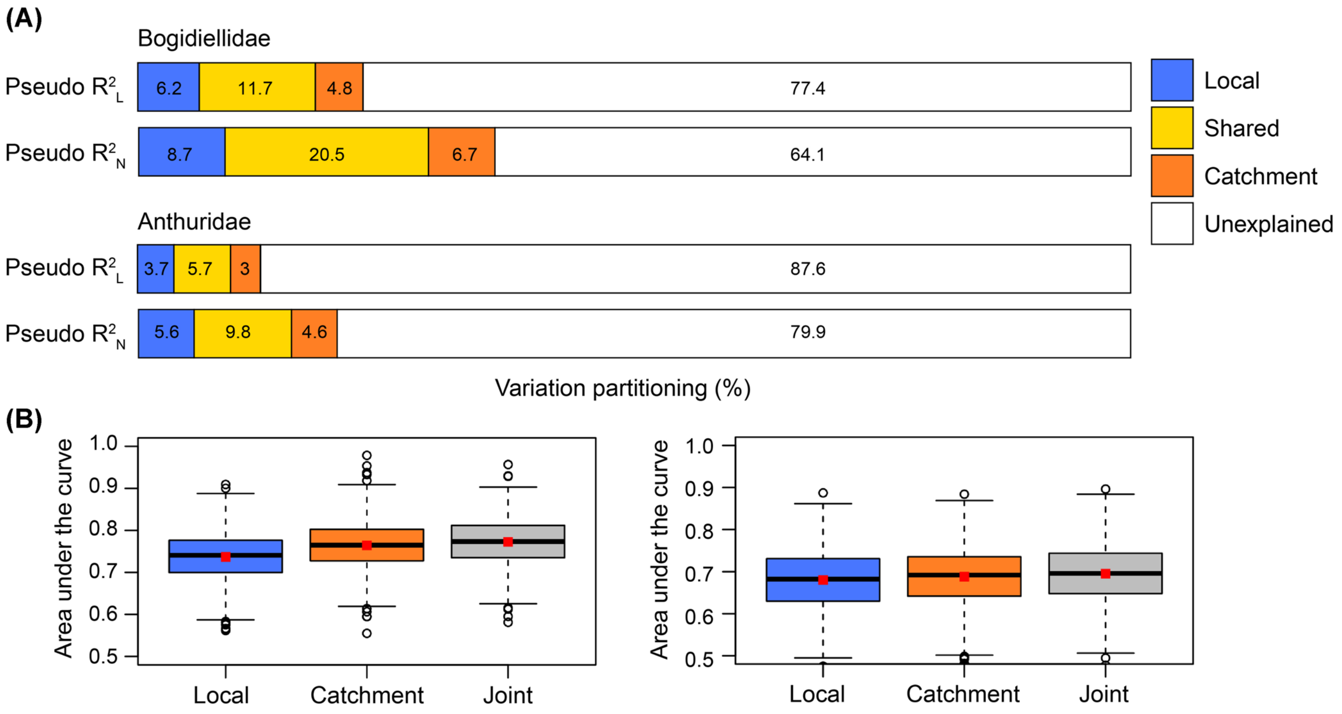

Figure 5. (A) Proportions of variation in the distribution of bogidiellids and anthurids in streams of New Caledonia explained by the unique and shared effects of local and catchment predictors. Variation partitioning with logistic regressions (Table 1) was performed using both the likelihood ratio pseudo R^2_L and the Nagelkerke's pseudo R^2_N. Results of variation partitioning using MacFadden's pseudo R^2 and Tjur's pseudo R^2 are shown in the Supporting information. (B) Predictive performance of the local, catchment and joint models for the bogidiellids (upper panel) and anthurids (lower panel) as assessed using 1000 random replicate values of the area under the curve (AUC) estimator. The black horizontal bars, red dots, boxes and open dots show the median, average, interquartile range and outliers, respectively ($n = 1000$ AUC values). The maximum length of each whisker is 1.5 × the interquartile range.

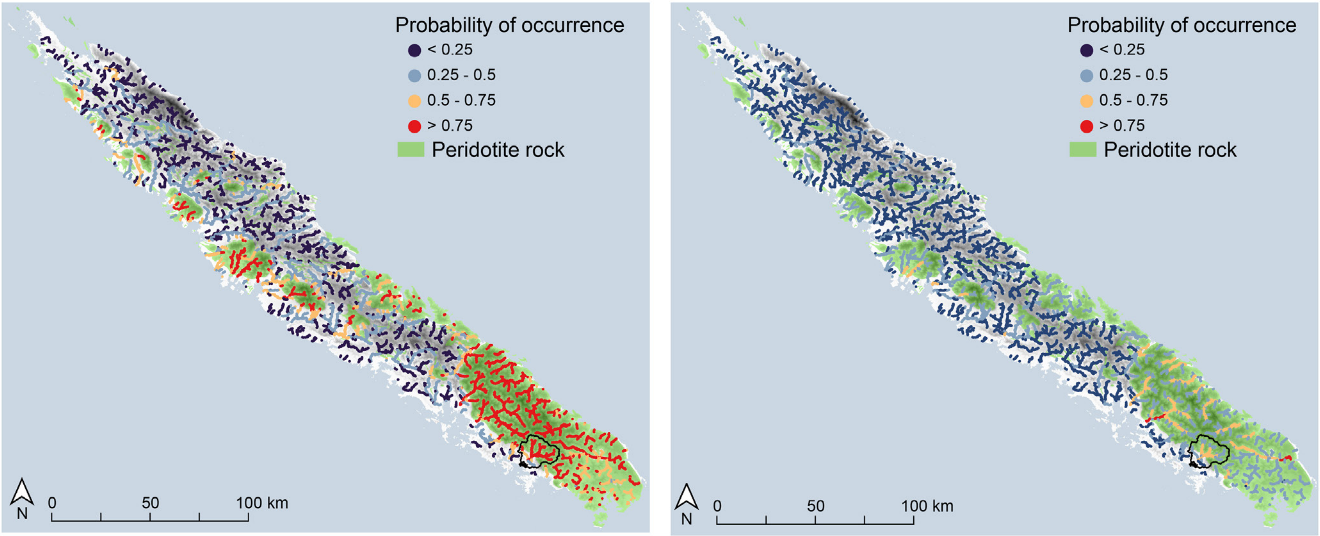

Figure 6. Maps of probability of occurrence of bogidiellids (left panel) and anthurids (right panel) in the stream network of New Caledonia generated with the catchment model. Probabilities were computed at 29 405 nodes regularly located at every 0.1-km² increase in catchment area from a minimum catchment area of five km². The black line corresponds to the boundary of the catchment shown in the Supporting information.

collinear predictors during model building (Dormann et al. 2013). From a statistical viewpoint, collinearity is considered as a case of model non-identifiability: a substantial amount of information is shared by collinear predictors and their effects cannot be separated (Dormann et al. 2013). However, we argue that collinearity and hence shared effects are intrinsic and readily interpretable features of stream networks: alluvial stream sites retain the biophysical imprints of the catchment from which they inherit sediment, water, organic matter and nutrients. We acknowledge that correlation between catchment and local predictors does not necessarily imply causation; hence, collinearity may not necessarily reflect indirect effects of catchment predictors. Variable selection requires an understanding of stream-catchment connections and hypotheses how these connections can drive species distributions. In the present study, the active channel width of alluvial streams – a proxy for the amount of hyporheic habitats – is positively related to catchment area ($r = 0.56$), even though local factors (i.e. valley confinement and riparian vegetation), the history of extreme floods and catchment lithological sensitivity to erosion may affect that relationship (Bertrand and Liébault 2019). Low flow stream discharge relative to catchment area increases with the areal proportion of peridotite ($r = 0.56$) because stream discharge is sustained by groundwater inputs from multilayer aquifer systems in peridotite rocks (Romieux and Wotling 2016, Jeanpert 2017). Hyporheic respiration also partly reflects catchment processes because it is subsidized by inputs of terrestrially derived organic carbon (Jones and Mulholland 2000, Fellows et al. 2001). We propose two non-mutually exclusive explanations for the strong positive relationships between DO, pH, redox potential of hyporheic water (i.e. sediment metabolism) and the areal proportion of peridotite rocks in catchments of New Caledonian streams. First, weak inputs of dissolved and particulate organic matter from ultramafic soils having low above-ground biomass may limit the consumption of DO and production of CO_2 by microbial communities (Mary 2002). Second, aquatic gross primary production and/or hyporheic microbial respiration may be constrained by the presence of easily leachable toxic metals, such as Cr(VI), in suspended and streambed sediments (Cervantes et al. 2001, Gunkel-Grillon et al. 2014).

Although local and catchment predictors are frequently used in SDMs (Chee and Elith 2012, Stewart-Koster et al. 2013, Kuemmerlen et al. 2014, Gies 2015, Fournier et al. 2017, Wellemeyer et al. 2019), we are unaware of any modelling studies that have explicitly partition the unique and shared effects of the two predictor types. This may connect to the way principles of hierarchy theory have been applied to stream networks (Melles et al. 2012). Variation partitioning is not applicable if stream networks are viewed as completely nested hierarchical systems, wherein multiple sites or stream segments are nested within a single catchment (Frissell et al. 1986, Snelder and Biggs 2002). Rather, it requires that stream networks are interpreted as directionally nested systems, wherein spatially overlapping catchments, each draining to a single site, accumulate hierarchically in a downstream direction (Frimpong et al. 2005, Seelbach et al. 2006, Chee and Elith 2012). We acknowledge that both the dependent variables (herein species occurrence) and predictors associated with overlapping catchments are not statistically independent but this an inherent consequence of directionally nested systems. Moreover, this difficulty was alleviated in the present study because many sites belonged to independent river catchments draining to the ocean. The lack of a comparable hierarchical framework and common variation-partitioning scheme among distribution modelling studies of freshwater taxa does not allow assessing the generality of our finding of a dominance of shared effects over unique effects of local and catchment predictors. This finding may owe much to the strong contrast in in-stream habitat conditions imposed by the presence of peridotite rocks, which is specific to New Caledonia. Yet, in the metacommunity literature, variation partitioning has become a standard approach for assessing the unique and shared effects of local habitat factors and regional, dispersal-related factors on the composition of aquatic communities (Smith and Lundholm 2010, Kuglerová et al. 2015, Cai et al. 2017, Li et al. 2021). Most, if not all, studies found that the variation accounted for by the shared fraction of local and spatial processes was considerably higher than their unique effects. For plants, Kuglerová et al. (2015) proposed that the dominant fraction of shared effects reflected the overwhelming influence of site position within the river network on both local processes and dispersal-related regional factors shaping communities.

A direct outcome of the dominance of shared effects was that the local and catchment predictors performed equally well in predicting the distribution of anthurids and bogidiellids. In both taxa, the local model explained slightly more variation than the catchment model, although its mean AUC value was not higher. Guidelines typically recommend selecting proximate factors that are closer to the mechanism along the sequence resource–direct–indirect predictors (Guisan and Zimmermann 2000, Franklin 2010, Dormann et al. 2013). However, for the purpose of prediction, distal catchment predictors may replace a combination of resource and direct gradients. In the present study, the amount of organic matter fueling stream metabolism probably decreased (resource gradient) and the availability of dissolved oxygen to hyporheic organisms increased (direct gradient) as the areal proportion of peridotite in the catchment increased (indirect gradient). In this respect, Mammola and Leroy (2018) identified some of the pitfalls of using indirect, surface predictors as proxy variables to model the distribution of subterranean organisms. This is because, often, surface variables are the only predictors available; although with inherent uncertainties, they can be used to generate predictions that are at least coherent with known expert-based distributions of these organisms (Mammola et al. 2018, 2019). Likewise, we took advantage of the tight connections between the hyporheic zone of streams and their catchment to provide predictions to unsampled locations for two subterranean taxa in difficult-to-access tropical streams of New Caledonia. Admittedly, our catchment-based prediction approach is sensitive to potential spatial changes in the pattern of collinearity among local and catchment predictors (Dormann et al. 2013, Gies 2015). Yet, such changes are unlikely here because predictions are restricted to the geographic domain of sampled data (i.e. interpolation). Moreover, we provided predictions at the local scale by developing a digital network of New Caledonian streams containing thousands of nodes, each of them associated with a catchment. Local predictions can be more readily validated by additional sampling than catchment-scale or grid-cell predictions. In addition, they can readily be integrated into planning tools to prioritize conservation or restoration efforts (Loiselle et al. 2003).

Our extensive sampling of the hyporheic zone on New Caledonian streams and model predictions considerably enlarged the distribution range of bogidiellids and anthurids, which had so far been reported from a handful of localities (Mary and Marmonier 2000, Jaume et al. 2007). Yet, bogidiellids and anthurids are essentially restricted to streams draining peridotite catchments. Anthurids are also more frequent in the most downstream and larger stream reaches, probably because these minute isopods are tightly associated with fine sediment particles. On-going taxonomic studies of collected specimens suggest that both taxa include several undescribed species. In several taxa including plants (Isnard et al. 2016), grasshoppers (Nattier et al. 2013) and aquatic caddisflies (Espeland and Johanson 2010), species radiation on peridotite substrates of New Caledonia was found to produce far more species than radiation on non-peridotitic substrates. The likely presence of several species within both taxa may in part account for the modest explanatory power and predictive performance of the distribution models if these species differ in their ecological niche (Qiao et al. 2017). Our finding that subterranean bogidiellids and anthurids are confined to the most oligotrophic streams of tropical New Caledonia contrasts with that of studies conducted in European temperate regions showing that the richness of subterranean crustaceans peaks in areas where productivity remained high over recent geological time (Eme et al. 2015, 2018, Zagmajster et al. 2018). This suggests that the relationship between productive energy and the richness of subterranean crustaceans can be hump-shaped (Strayer et al. 1997, Eme et al. 2015). Species richness increases with increasing organic matter supply until DO deficiency caused by microbial respiration becomes a limiting factor.

Conclusion

Although 'the valley rules the stream' hypothesis (Hynes 1975) emerged as a central tenet of stream ecology, it may not have been fully integrated into empirical studies of species' distributions. If Hynes' hypothesis holds true beyond the present study, then neither local or catchment predictors would be expected to have a much better explanatory power. Systematically partitioning the unique and shared effects of the two predictor types – a common practice in stream metacommunity studies (Keck et al. 2018, Li et al. 2021) – can provide a more holistic understanding of cross-scale drivers of species distributions than searching for evidence to support a particular predictor type. It can also provide a useful cross-study comparison framework for identifying the general mechanisms causing the unique effect of one predictor type to be dominant. Variation in past climatic and/or hydrological disturbances among catchments with similar present-day local habitat conditions may result in a strong contribution of unique effects of catchment predictors among taxa with reduced dispersal ability (Castellarini et al. 2007, Foulquier et al. 2008). At last, it may stimulate modelling of species occurrences for biodiversity assessment in disciplines where local predictors are difficult to acquire and the use of indirect predictors is problematic (Mammola and Leroy 2018, Araújo et al. 2019).

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Author contributions

Samuel Mouron: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Writing – original draft (lead); Writing – review and editing (equal). **David Eme**: Conceptualization (equal); Formal analysis (lead); Writing – original draft (supporting); Writing – review and editing (equal). **Arnaud Bellec**: Investigation (supporting); Resources (supporting); Writing – review and editing (equal). **Mélanie Bertrand**: Investigation (supporting); Resources (supporting); Writing – review and editing

(equal). **Stefano Mammola**: Formal analysis (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Frédéric Liébault**: Investigation (supporting); Resources (supporting); Writing – review and editing (equal). **Christophe J. Douady**: Conceptualization (equal); Funding acquisition (lead); Investigation (equal); Supervision (supporting); Writing – review and editing (equal). **Florian Malard**: Conceptualization (equal); Investigation (lead); Project administration (lead); Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal).

Transparent Peer Review

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.qrfj6q5hv> (Mouron et al. 2022a), and scripts are available from the Zenodo Repository: <https://zenodo.org/record/6104368#.YhNgiujMKUk> (Mouron et al. 2022b).

Supporting information

The supporting information associated with this article is available from the online version.

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